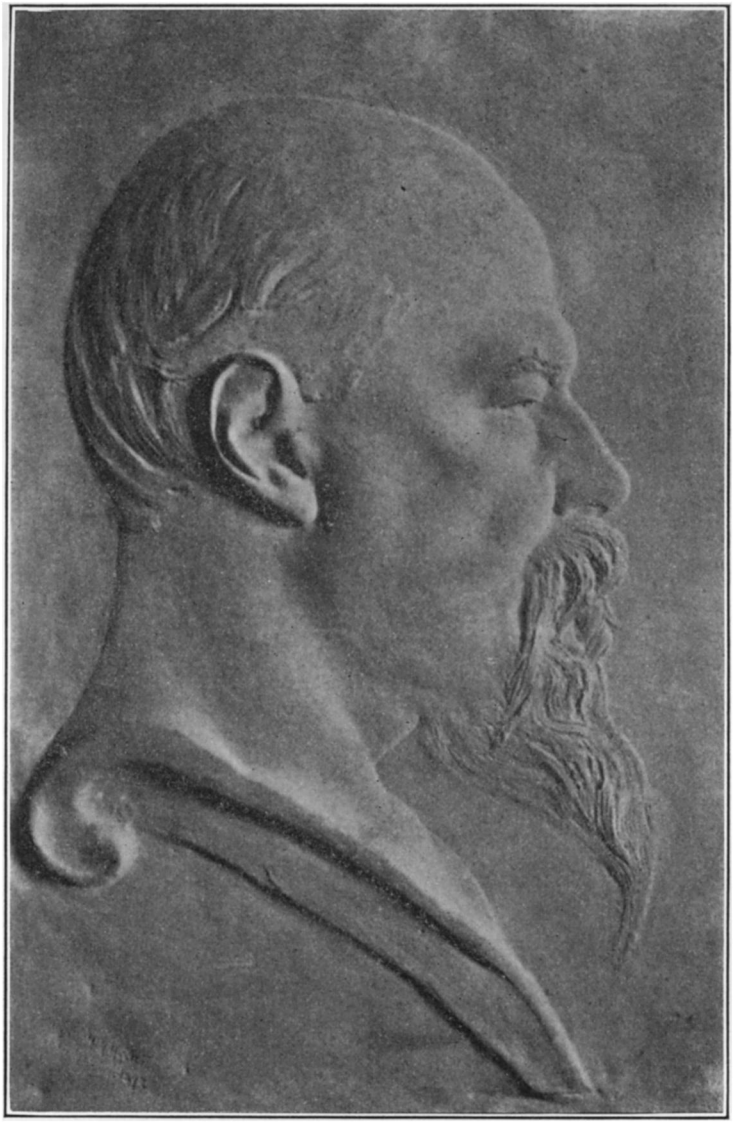

PROFESSOR ALPHEUS HYATT.

THE

AMERICAN NATURALIST

VOL. XLVII *April, 1913* No. 556

ALPHEUS HYATT AND HIS PRINCIPLES OF RESEARCH[1]

DR. ROBERT TRACY JACKSON
BOSTON

PROFESSOR HYATT devoted his life to pure science in the best sense of the word. While known primarily for his work on fossil cephalopods, in his researches he covered a wide range of groups, doing critical work on sponges, bryozoans, pelecypods, gastropods, cephalopods and insects. He also published a number of purely philosophical papers on his subject. He taught zoology and palæontology, was a museum administrator, an organizer of societies, and maintained a seaside laboratory at Annisquam, Mass. He was fond of social life and was a most genial and charming host. With strong personal feelings and convictions, he was remarkably tolerant of differences of opinion. One of the most approachable of men, he was very kind and considerate to young men. The accompanying portrait is from a bas-relief made by Professor Hyatt's daughter, now the wife of Dr. Alfred G. Mayer.

Professor Hyatt was essentially philosophical in all his work, and his researches were largely devoted to evolutionary problems. His publications contain most important conclusions and generalizations. He discovered new principles and greatly expanded the principles of others, so that he was justly considered the founder of

[1] A paper given before the Palæontological Society of America, at the New Haven meeting, December, 1912.

a school of evolutionary research. A leader in this school was the late Charles Emerson Beecher, an eminent professor in Yale University. I wish to point out briefly what these principles are, and their application, but without going into the question of who first enunciated the principles, which is often difficult to ascertain. For the present purpose it is sufficient to consider them as the principles that Hyatt made use of and welded into a component whole for phylogenetic investigation.

It was my privilege to be intimately associated with Professor Hyatt as a student and assistant from 1886, until his death, in 1902, and I can not too strongly express the help and pleasure derived from his boundless enthusiasm, ever ready sympathy and wise counsel. He was laborious and painstaking in his work, constantly urged the importance of large series of individuals for study, and the importance of the bearing of abnormal or pathological specimens. The value of a specimen to him was for what it showed, by itself, and in its relation to associated forms. He urged the comparative study of young and adult, living and fossil forms in a united study. To a zoologist the only difference that should be recognized between living and fossil animals is the condition of preservation and the time element. A study of the recent throws light upon the fossil, and conversely a study of the fossil throws light upon the recent. A united study of both recent and fossil gives a grasp upon a group that can not be attained from either alone.

Stages in development were constantly uppermost in Professor Hyatt's mind, not stages in the embryo only, which are the main conception of stages to most zoologists, but stages throughout the life of the individual, from the egg to the adult and old age. It was the later, or postembryonic, stages that he especially urged the importance of to the phylogenist, and he demonstrated that these later stages possess characters which are directly comparable to the adult condition of related forms. In other words, that the ontogeny of the indi-

vidual gives in abbreviated form a recapitulation of the phylogeny of the group. This is the law of morphogenesis of Hyatt[2] by which he endeavored to demonstrate that a natural classification may be made by a system of analysis in which the individual is the unit of comparison, because its life in all its phases, morphological and physiological, healthy or pathological, embryo, larva, adolescent, adult and old (ontogeny), correlates with the morphological and physiological history of the group to which it belongs (phylogeny).

To the student of invertebrate fossils these animals present certain advantages, not only on account of their relative abundance, but also because, in many forms at least, from the study of a single specimen, one can gather in a more or less complete degree the stages through which it has passed in development. As Hyatt[3] says:

> How unreasonable it would seem to a student of fossil Mammalia, if he were requested to do what it would be appropriate to require from a student of fossil Cephalopoda, viz., to describe from the investigation of a single perfect fossil skeleton of an adult, not only the characteristics of the skeleton at the stage of growth at which the animal died, but the developmental stages of this same skeleton, and in case it were the remains of an old, outgrown animal, also, the retrograde metamorphoses through which it had passed during its last stages of decline. It might require a lifetime to make out the stages of a single species of mammal satisfactorily from the isolated specimens which would be found and the attempt would be hopeless for all the youngest stages of growth, while the bones were still cartilaginous. This kind of evidence, however, is readily obtainable among fossil Cephalopods . . . and it can be obtained in good collections everywhere.

While this is especially true of the tetrabranchiate cephalopods, it is also true in a more or less complete degree of some other groups of molluscs, as well as many brachiopods, echinoderms and corals.

As examples of types showing stages in development, the following may be cited. The living *Nautilus* has a close-coiled shell, but in its development passes through

[2] A. Hyatt, "Genesis of the Arietidæ," Smithsonian Contributions to Knowledge, Washington, 1889.

[3] A. Hyatt, "Phylogeny of an Acquired Characteristic," *Proc. Amer. Phil. Soc.*, Vol. 32, 1894.

arcuate, loose-coiled, then close-coiled stages directly comparable to the adults of Paleozoic cyrtoceran, gyroceran and nautiloid representatives of its own group. As shown by J. Perrin Smith,[4] the highly evolved Cretaceous *Placenticeras pacificum* which in the adult has complex sutures, in the development of these parts passes through simpler stages which are comparable to the adult structures of nautiloid, goniatitic and glyphioceran forms, followed by stages in which the septa are comparable to those of early *Ammonites,* before it assumes its adult generic features. The recent *Pecten* has strongly marked ears, but the young shell is strikingly different, first having a rounded nuculoid form, followed successively by *Rhombopteria, Pterinopecten* and *Aviculopecten* stages before its adult character is attained. In Echini the recent *Goniocidaris* and other genera, both recent and fossil, have two or more columns of plates in each interambulacral area, but in the young they pass through a stage in which there is a single plate at the ventral border of the interambulacra, which is comparable as a stage in development to the adult of the Ordovician *Bothriocidaris* which retains a single column of plates in each interambulacral area in the adult. The Lower Carboniferous echinoid *Oligoporus* which in each ambulacrum has four columns of plates with, in addition, scattered isolated plates, passes through stages with primary plates only, as in *Palæechinus,* then primary and occluded plates as in *Maccoya,* followed by four columns, without isolated plates, as in *Lovenechinus,* before attaining its generic character. In Brachiopoda, as shown abundantly by Beecher and others, stages in development are shown in the exterior and interior of the shell and the brachial supports which can be closely correlated with adult characters of more primitive representatives in the group.

While stages in development from the young to the adult are typically all progressive, in senescence, the

[4] J. P. Smith, "The Development and Phylogeny of Placenticeras," *Proc. California Acad. Sci.*, Ser. 3, Geology, Vol. 1, No. 7, 1900.

stages that appear are in the main regressive. Nautiloids and ammonoids, which are characterized by close-coiled shells, build loose-coiled or even uncoiled additions; specialized *Ammonites* with complex septa, in senescence build simpler septa. Palæozoic Echini, which are characterized by many columns of plates in an interambulacral area, lose some of these columns in old age growth, all in these features taking on simpler characters comparable to those seen in their own youth, and also comparable to the characters of adults in regressive series in their own groups.

As an aid in describing stages, Professor Hyatt[5] devised a classification of stages in development and decline which is a great convenience in exact description. In this classification the ontogeny is primarily divided into embryonic and postembryonic periods, the latter being for the most part the more important in phylogenetic work. Of embryonic stages the *protembryo* is represented by the egg and segmentation stages of the same, comparable to the simple and colonial Protozoa as adult forms. The *mesembryo* is the blastula stage, with a single layer of cells on the periphery of a hollow sphere, comparable to *Volvox* and *Eudorina,* the Mesozoa of Hyatt. The *metembryo* is the gastrula stage, comparable to the simplest of the sponges. The *neoembryo* is a later stage represented by the early ciliated cephalula stage of a brachiopod and the trochosphere of a mollusc, comparable to the embryo of chætopod worms and other Cœlomata. The *typembryo* is that stage in development when the features of the great group to which the animal belongs appear. In Mollusca the shell gland and plate-like beginnings of the shell appear at this stage. In brachiopods, two folds of the second segment of the embryo turn forward and the corneous shell begins to appear. The *phylembryo* is the completed embryonic stage and is the first ontogenetic stage that is applicable

[5] A. Hyatt, "Values in Classification of the Stages of Growth and Decline with Propositions for a New Nomenclature." [Somewhat altered in later publications. R. T. J.] *Proc. Boston Soc. Nat. Hist.*, Vol 23, 1888.

in palæontological study. It is the stage in which the characters of the class to which the animal belongs are established. This period is represented by the protechinus of Echini, the protegulum of Brachiopoda, the prodissoconch of Pelecypoda, the protœcium of Bryozoa, the protoconch of Cephalous Mollusca and the protaspis of the Tritobita. This stage in development is represented in fossil as well as living forms in many types, and the primitive radicle that it represents as a phylogenetic stage has been pointed out as *Paterina* for the Brachiopoda by Beecher, as a nuculoid type for certain Pelecypoda, and as *Bothriocidaris* for the whole class of Echini by Jackson.

Of postembryonic stages the first are the *nepionic* or babyhood stages, abundantly recognizable in fossil as well as recent types. Succeeding these are the *neanic,* or youthful stages. The *ephebic* is the adult, or that stage in which the full species characters are evinced. Senescence or old age is expressed in *gerontic* stages, in which appear the loss of characteristic species features, and by such loss an approach is commonly made to the youthful character before such features are attained. Gerontic stages while in a measure repeating youthful characters, do so in the inverse order to that in which they are acquired in ontogeny. As shown abundantly by Hyatt, senescent features are prophetic of the adult characters in regressive series of the group.

In studies of ontogeny it often occurs that stages need to be further subdivided. For this purpose Professor Hyatt introduced the prefixes *ana, meta* and *para,* so that one can speak of the *ananepionic, metanepionic* or *paranepionic* stage of *Nautilus,* etc. By means of this simple nomenclature the life stages of any organism are divisible into ten main or thirty minor periods, which are thus readily and clearly expressed.

In ontogeny, as shown by overwhelming evidence, the organism passes through stages which repeat the characters of adults of more primitive types in serial order, and it is believed that this serial order may be safely

accepted as a recapitulation of the phylogeny of the group in hand. Stages are not equally clear in all types, for stages may be skipped, or may be telescoped in specialized forms, but in primitive forms (*Nautilus, Lingula, Pecten, Cidaris*) they are astonishingly clear and complete. By some investigators stages have been denied and the recapitulation theory considered a myth. I can not enter into discussion here, but can simply say that it is felt that opponents have not considered the evidence. Cumings[6] has recently put the matter well in a defence of the Recapitulation Theory.

The principle of acceleration of development, originated by Professor Hyatt,[7] is at once an explanation of the existence of stages in development, and the loss, or skipping of stages as well. This principle maintains that features appearing at or near the adult period of development are inherited at earlier and earlier stages in successive generations until they exist only in the extreme young or are skipped as stages in development.

As examples of accelerations: In certain Palæozoic Echini the full number of columns of ambulacral and interambulacral plates are attained only in the adult. In more specialized species the similar columns are taken on much earlier in both areas than they appear in lower species (*Melonechinus*). The pelecypod *Hinnites* is attached by the fixation of one valve to foreign objects when about one fourth grown, and then loses its young pecteniform character. The allied *Spondylus* is attached when very much younger and thus earlier loses the similar stage. *Plicatula* is attached at the close of the prodissoconch stage and has lost the pecteniform stage altogether. In primitive tritobites (*Solenopleura, Sao*) the protaspis is rounded with neither dorsal eyes nor

[6] E. R. Cumings, "Palæontology and the Recapitulation Theory," *Proc. Indiana Acad. Sci.*, twenty-fifth anniversary meeting, 1909.

[7] A. Hyatt, "On Parallelism between the Different Stages of Life in the Individual and Those in the Entire Group of the Molluscous Order Tetrabranchiata," *Mem. Boston Soc. Nat. Hist.*, Vol. 1, 1866, p. 203. See also [minutes of meeting of February 21, 1866] *Proc. Boston Soc. Nat. Hist.*, Vol. 10, pp. 302–303.

ornamentation. In the specialized genera *Acidaspis* and *Arges,* as shown by Beecher, both dorsal eyes and denticulate ornamentations occur in the protaspis.

In acceleration of development, when skipping of stages occurs, it is not the earliest or embryonic stages that are skipped, but later or postembryonic. Embryonic stages are clung to with striking pertinacity. Stages are often run together or telescoped as expressed by Grabau,[8] when in a specialized type more than one phase may be represented at a single stage, although such stages are clearly distinct in more primitive types.

As an outgrowth of Professor Hyatt's studies of stages in development, the principle of colonial development has been enunciated independently by Ruedemann[9] in Graptolites, by Cumings[10] in Bryozoa and by Lang[11] also in Bryozoa. These investigators show that in the growth of the colony there are distinct stages in development which can be correlated with the adult characters of more primitive colonial forms. In this respect the colony behaves as an individual. Cumings introduces the terms nepiastic, neanastic, ephebastic, gerontastic as descriptive adjectives of these colonial stages. It is felt that this special nomenclature for colonial stages is unnecessary and therefore undesirable, because the simpler the terminology can be kept in such work, the more likely it is to be widely accepted and made use of.

Another phase of stages is localized stages in development in which I[12] showed that throughout the life of the individual stages may be found in localized parts which

[8] A. W. Grabau, "Studies of Gastropoda. III. On Orthogenetic Variation," AMER. NATURALIST, Vol. 41, 1907.

[9] R. Ruedemann, "Growth and Development of *Goniograptus thureaui* M'Coy," *Bull. N. Y. State Mus.*, No. 52, 1902.

R. Ruedemann, "Graptolites of New York." Pt. 1, *Mem. N. Y. State Mus.*, No. 7, 1904. Pt. 2, *idem,* No. 11, 1904.

[10] E. R. Cumings, "Development of Some Palæozoic Bryozoa," *Amer. Journ. Sci.* (4), Vol. 17, 1904.

[11] W. D. Lang, "The Jurassic Form of the 'Genera' *Stomatopora* and *Proboscina*," *Geol. Mag.*, dec. 5, Vol. 1, 1904.

[12] R. T. Jackson, "Localized Stages in Development in Plants and Animals," *Mem. Boston Soc. Nat. Hist.*, Vol. 5, 1899.

repeat the characters seen in youth and in the adults of more primitive types. Such localized stages are shown by many trees and other plants. In the oak, ash and hickory, suckers from the base of the tree have simple forms of leaves, comparable to those seen in young seedlings. Beneath the flower (rose, peony), at the tips of branches (hickory, sassafras) and in diseased or feeble growths (tulip-tree, red cedar) leaves often occur which in simplicity of character are comparable to those of seedlings or more primitive species in the group. Localized stages occur also in herbaceous plants as shown by Cushman.[13]

Amongst animals localized stages are shown where during growth there is an addition of similar parts as the plates in echinoderms, septa in cephalopods and in the developing zooids of colonies of corals and, according to Ruedemann, in Graptolites. In these types the parts as added present stages which are comparable to stages seen in the ontogenesis of the individual as a whole. In Echini new plates are added to the corona immediately below the oculars, and at this region throughout life the ambulacral plates are of a simple character, whereas the older earlier formed plates during their individual development may have taken on complex characters, for example, in *Centrechinus* (*Diadema*) ambulacral plates are compound, but close to the oculars are simple. In the Palæozoic family of the Palæechinidæ, the ambulacrum at the equator, or midzone, has from two to twelve columns of plates in each area, but in those genera with many columns there are only two columns dorsally in the area where new plates are added. In crinoids, in which the arms have the plates arranged in a biserial manner (*Encrinus, Platycrinus*) as shown by Grabau,[14] a uniserial arrangement exists at the tips

[13] J. A. Cushman, "Studies of Localized Stages of Growth in Some Common New England Plants," AMER. NATURALIST, 1902; *idem*, "Studies of Localized Stages in Some Plants of the Botanic Gardens of Harvard University," AMER. NATURALIST, 1903.

[14] A. W. Grabau, "Notes on the Development of the Biserial Arms in Certain Crinoids," *Amer. Journ. Sci.* (4), Vol. 16, 1903.

where the young plates are added. In *Ammonites,* as *Placenticeras,* in which the sutures of the septa are complex, often in a very high degree, we find that at the inner, or umbilical, portion of each individual septum a simpler condition exists, and greater complexity is attained in passing from the ventral portion of the septum outward, or dorsally. This simpler ventral portion in an adult can be compared with the simpler condition in a whole septum of the young, or with the septum of the adult in a more primitive and geologically older representative of the group.

Parallelism is a most important principle and was constantly used by Professor Hyatt in his studies. Parallelism is the taking on of a similar form in independent lines of descent. It may help one in explaining the origin of structures, but is sometimes confusing as indicating a basis of relationship which is misleading. In Crustacea the recent isopod *Serolis* closely resembles a trilobite. The uncoiled gastropod shell *Vermetus* closely resembles the worm *Serpula. Spondylus, Chama* and *Müllleria* amongst Pelecypoda, and *Davidsonella* and *Derbya* among Brachiopoda are all attached by the calcareous fixation of one valve and closely resemble *Ostrea,* which has a similar habit of life. The complex septa of the Tertiary nautiloid *Aturia* closely resemble those of the Devonian ammonoid *Goniatites.* Echini with imbricating coronal plates were considered as related on account of this character, but this structure appears in several independent lines in the group. The recent deep-sea Echinothuriidæ have many rows of ambulacral plates only in the peristome. By this character they have been associated with the Palæozoic Lepidocentridæ which have the same feature. I believe however that it is purely a parallelism and not a basis for genetic connection.

Larval adaptation is the term applied to special features built up as youthful adaptations and which are not, therefore, of phylogenetic significance. Such adaptations are a marked feature of certain groups as the ventral spurs developed in the embryonic glochidial stage of

the Unionidæ. Larval adaptations are most marked in the youthful stages of some insects, as in caterpillars. In most invertebrates, however, at least in postembryonic stages, larval adaptations are uncommon and can usually be eliminated as a factor in studying ontogenetic stages.

The Hyatt principles have been used as a working basis in the phylogenetic classification of three entire classes of animals, the Brachiopoda and Trilobita by Beecher[15] and the Echini by myself.[16] They have also been used as a basis of partial classifications of Cephalopoda by Hyatt himself, of Protozoa by Cushman,[17] of Pelecypoda by Jackson,[18] of Gastropoda by Grabau,[19] and also to a certain extent in suggesting genetic relationships in a number of other groups of animals and in plants by various investigators.

If I may be permitted to speak of my own studies, I have recently completed a phylogenetic study of the Echini, and throughout the work made use of the Hyatt principles. In this use there was no occasion to qualify a single one. To work out principles largely on one group (the Cephalopoda) as did Hyatt, and then to have his followers apply these principles successfully to many widely separate groups, and even to seek and ascertain facts on the basis of the implied principles, is strong evidence that he got at fundamental truths.

At present the phylogeny of invertebrates is little studied, palæontologists are largely occupied with questions of stratigraphy, and zoologists occupy themselves with other lines of work. In future, as phylogenetic work is prosecuted, I believe that Hyatt will be looked on as the master mind who pointed out the methods by which to ascertain the true phylogenetic relations of invertebrate organic forms.

[15] C. E. Beecher, "Studies in Evolution," New York, 1901.

[16] R. T. Jackson, "Phylogeny of the Echini," *Mem. Boston Soc. Nat. Hist.*, Vol. 7, 1912.

[17] J. A. Cushman, "Developmental Stages in the Lagenidæ," AMER. NATURALIST, Vol 39, 1905.

[18] R. T. Jackson, "Phylogeny of the Pelecypoda," *Mem. Boston Soc. Nat. Hist.*, Vol. 4, 1890.

[19] A. W. Grabau, "Phylogeny of *Fusus* and Its Allies," Smithsonian Misc. Coll., Vol. 44, 1904.